Habitat characteristics provide insights of carbon storage in seagrass meadows

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A B S T R A C T

Seagrass meadows provide multiple ecosystem services, yet they are among the most threatened ecosystems on earth. Because of their role as carbon sinks, protection and restoration of seagrass meadows contribute to climate change mitigation. Blue Carbon strategies aim to enhance CO_2 sequestration and avoid greenhouse gasses emissions through the management of coastal vegetated ecosystems, including seagrass meadows. The implementation of Blue Carbon strategies requires a good understanding of the habitat characteristics that influence C_{org} sequestration. Here, we review the existing knowledge on Blue Carbon research in seagrass meadows to identify the key habitat characteristics that influence C_{org} sequestration in seagrass meadows, those factors that threaten this function and those with unclear effects. We demonstrate that not all seagrass habitats have the same potential, identify research priorities and describe the implications of the results found for the implementation and development of efficient Blue Carbon strategies based on seagrass meadows.

1. Introduction

Meeting the commitments made in the CoP21 meeting (Paris Agreement) requires climate change mitigation through a reduction of CO_2 emissions and an increase in carbon sequestration (Rogelj et al., 2016). Among carbon sequestration strategies is the enhancement of ecosystems that act as natural carbon sinks, when CO_2 absorbed through photosynthesis and stored as biomass (organic carbon, C_{org}) is greater than that released through respiration and decomposition (Trumper et al., 2009). Coastal vegetated ecosystems (i.e. tidal marshes, mangroves and seagrasses) are among the most significant natural carbon sinks (Smith, 1981; Duarte et al., 2005). Yet, they have been often neglected in the global carbon cycle models and not considered within the traditional greenhouse gasses (GHG) abatement schemes (Macreadie et al., 2014; Duarte, 2017). The publication of two reports (Laffoley and Grimsditch, 2009; Nellemann et al., 2009) building on the demonstration of their relevance as carbon sinks at a global scale (Duarte et al., 2005) triggered the development of climate change

mitigation strategies based on their protection and restoration, similar to those already existing for terrestrial ecosystems (e.g. REDD+ program). The organic carbon sequestered by coastal vegetated ecosystems has been termed Blue Carbon and the initiatives to mitigate climate change through their protection and restoration are known as Blue Carbon strategies (Nellemann et al., 2009).

Seagrass meadows are especially relevant due to their global distribution and large aerial extent (Hemminga and Duarte, 2000; Chmura et al., 2003). The largest C_{org} deposits in seagrass meadows are located in the soil compartment, formed by refractory belowground biomass, seagrass detritus and allochthonous C_{org} embedded in the soil matrix (Gacia et al., 2002; Kennedy et al., 2010). Due to the anoxic conditions of the sediment, soil C_{org} deposits may remain for millennia, constituting long-term carbon sinks (Mateo et al., 2006). On the contrary, seagrass above-ground biomass, which is more labile than belowground biomass due to their exposure to aerobic conditions and herbivory and their more labile chemical composition (Enriquez et al., 1993), is considered a short-term carbon sink and has a low

contribution to the total C_{org} deposits found in seagrass meadows (Mateo et al., 2006; Fourqurean et al., 2012). In addition to C_{org} sequestration, seagrass meadows provide multiple other ecosystem services critical for coastal communities, including support of fisheries, the improvement of water quality, coastal protection and cultural services, and they are considered among the most valuable ecosystems on earth (Costanza et al., 1997; Nordlund et al., 2017). Seagrass meadows are, however, experiencing a global decline (Waycott et al., 2009), leading to the loss of all the ecosystem services they provide including C_{org} sequestration, and potentially leading to CO_2 emissions when soil C_{org} deposits are eroded and exposed to aerobic conditions (Marbà et al., 2014; Serrano et al., 2016; Lovelock et al., 2017).

The significant role that seagrass meadows play as carbon sinks opens new opportunities for coastal managers to promote their conservation and restoration as a strategy to mitigate climate change. For instance, Blue Carbon can be used as a tool to access carbon financing and compensate part of the costs for the protection and restoration of seagrass meadows, contribute to national GHG emission reduction targets and be incorporated as an additional benefit to enhance the creation of marine protected (Adame et al., 2015; Herr and Landis, 2016; Herr et al., 2017; Howard et al., 2017). However, soil C_{org} stocks and sequestration rates are highly variable among seagrass species and sites (Lavery et al., 2013; Miyajima et al., 2015; Mazarrasa et al., 2017a). The use of Blue Carbon as a tool for climate change mitigation or conservation purposes requires considering this variability and to identify areas which may become important CO_2 sources in the future (Herr et al., 2015, 2017). Thus, a robust understanding of the factors that enhance or inhibit C_{org} sequestration and storage in seagrass soils as well as those that may cause CO_2 emissions following disturbance and subsequent remineralization of soil C_{org} deposits is needed.

Seagrass meadows develop across a wide range of climatic regions (from tropical to high temperate latitudes) and habitat types (from sheltered bays and estuaries to highly exposed areas), and from the intertidal zone to 40 m depth (Duarte, 1991a; Carruthers et al., 2007). These different habitats are characterized by different environmental factors. For example, they vary in terms of temperature, hydrodynamic energy, light availability and turbidity, which determines meadow biotic characteristics, such as species composition, structural and physiological traits (e.g. density, cover, biomass allocation and productivity) (Alcoverro et al., 2001; Carruthers et al., 2007) and abiotic parameters, such as the load of allochthonous C_{org} in the water column, the depositional vs. erosional nature of the meadow and the sedimentation rates (Carruthers et al., 2007). All these habitat characteristics influence the sequestration and storage of C_{org} in seagrass soils as demonstrated in recent studies (Lavery et al., 2013; Serrano et al., 2014; Samper-Villarreal et al., 2016; Serrano et al., 2016). In addition, seagrass habitats are expected to change in the near future due to consequences of climate change, including increasing temperature, ocean acidification and sea level rise, and also due to the intensification of human pressure in coastal areas. It is unclear what effect this will have on the global carbon sink capacity of seagrass meadows (Duarte, 2002; UNEP, CIFOR, 2014).

Despite the increasing number of studies assessing the role of habitat characteristics on C_{org} stocks and sequestration rates in seagrass soils, information remains sparse and difficult to apply for management purposes due to: a limited number of habitat characteristics assessed in each study; the different spatial scales at which factors influence C_{org} sequestration, from large regions (e.g. climatic region; Lavery et al., 2013; Miyajima et al., 2015) to regional scales across different meadows (i.e. hydrodynamic energy, turbidity, canopy complexity) (Samper-Villarreal et al., 2016; Mazarrasa et al., 2017a) or to small spatial scales within the same meadow (e.g. water depth gradient, Serrano et al., 2014); and the contradictory results found among different studies regarding some habitat characteristics (i.e. water depth; Lavery et al., 2013; Serrano et al., 2014; Mazarrasa et al., 2017a), which points to potential interactions among factors.

Here we aim to identify and synthesize the key habitat characteristics that influence long-term C_{org} sequestration in seagrass meadows. Our analysis is based on the current knowledge of seagrass ecology and on a review of the most recent literature on Blue Carbon research (Table S1). Firstly, we review the main mechanisms that lead to C_{org} sequestration in seagrass soils. Then we describe how variation in habitat characteristics, both biotic and abiotic, influences those mechanisms and thus C_{org} sequestration and how climate change and human pressure may affect this process. We provide guidance for the identification of habitats where C_{org} sequestration is enhanced and habitats where this function is reduced or even threatened. Finally, we identify key research priorities and describe the implications of the results found in this study for the implementation and development of Blue Carbon strategies in seagrass meadows.

2. Mechanisms enhancing Blue Carbon storage in seagrass meadows

Seagrass meadows sequester both autochthonous and allochthonous C_{org}. Autochthonous C_{org} is composed of above-ground (i.e. shoots and leaves) and below-ground (i.e. roots and rhizomes) biomass, and seagrass detritus accumulated in the soil. Allochthonous C_{org} refers to non-seagrass carbon deposited mainly from the water column (e.g. sestonic carbon) (Kennedy et al., 2010) which is enhanced by the presence of the seagrass canopy (Gacia et al., 2002; Hendriks et al., 2008). Allochthonous C_{org}, particularly that derived from macroalgae and phytoplankton, is much more labile than seagrass C_{org}, especially compared to below-ground biomass (Enriquez et al., 1993; Klap et al., 2000; Banta et al., 2004). Yet, once incorporated within the soil compartment, where low oxygen levels inhibit microbial activity (Trevathan-Tackett et al., 2017), remineralization of allochthonous C_{org} is reduced, leading to a significant contribution to the long-term C_{org} deposits that develop in seagrass soils (global average of 50%; Kennedy et al., 2010).

In addition, by favoring particle sedimentation, seagrass meadows tend to enhance the formation of muddy soils (Gacia et al., 2002; Hendriks et al., 2008; Dahl et al., 2016; Serrano et al., 2016). A high mud content in seagrass soils has been demonstrated to reduce remineralization of organic C_{org} by enhancing soil anoxic conditions (lowering permeability and oxygen penetration) and by protecting organic particles from microbial action following absorption to fine mineral particles (Kell et al., 1994; Mayer, 1994; Burdige, 2007; Serrano et al., 2016; Miyajima et al., 2017).

Hence, the formation of sedimentary C_{org} deposits in seagrass meadows relies on three main processes: seagrass meadow productivity and biomass accumulation (particularly below-ground tissue); the input of allochthonous C_{org} into the sediment compartment; and the C_{org} burial efficiency in seagrass sediments, which is enhanced by the anoxic conditions of the sediments, the mud content and the proportion of refractory C_{org} being stored (e.g. the relative contribution of autochthonous and allochthonous C_{org}) (Mateo et al., 2006; Serrano et al., 2016). Thus, seagrass habitats where those three processes concur (seagrass biomass accumulation, allochthonous C_{org} sedimentation and C_{org} burial efficiency) will have the largest potential for C_{org} sequestration and storage. In the following section, we describe the expected effect of different habitat characteristics on seagrass biomass accumulation, allochthonous C_{org} sedimentation and/or C_{org} burial efficiency and, as a consequence, on the capacity of seagrass meadows for C_{org} sequestration and storage.

3. Effect of habitat characteristics on the long-term C_{org} sequestration in seagrass soils

3.1. Biotic factors

3.1.1. Species composition

Seagrass species are highly variable in terms of size, biomass,

biomass distribution and dynamic features such as life span, primary productivity and turnover rates, resulting in different ecological roles (Den Hartog, 1977; Duarte, 1991b; Duarte and Chiscano, 1999). In general, small species (e.g. *Halophila* spp. and *Halodule* spp.) are typical "colonizers", having high growth and turnover rates, which leads to lower biomass accumulation than larger and long-lived 'persistent' species (e.g. *Posidonia* spp. and *Thalassia* spp.) (Duarte and Chiscano, 1999; Kilminster et al., 2015; Serrano et al., 2016). In addition, larger seagrasses species have higher below-ground: above-ground biomass ratios than smaller species (Duarte and Chiscano, 1999). This variation in biomass allocation enhances the efficiency of preservation of the autochthonous C_{org} due to the proximity of this material to anoxic conditions in seagrass soils and the more refractory nature of below-ground tissues (e.g. enriched in lignin) compared to above-ground tissues (Klap et al., 2000; Fourqurean and Schrlau, 2003). Furthermore, lignin content seems to be higher in long-lived and large seagrass species (Duarte, 1991b; Klap et al., 2000).

At the same time, the capacity of seagrass meadows to reduce hydrodynamic energy from currents, waves and tides, generally increases as leaf size increases and the percentage of the water column occupied by the seagrass canopy increases (Fonseca and Fisher, 1986; Fonseca and Cahalan, 1992). Thus, meadows formed by large seagrass species are expected to be more effective at enhancing particle sedimentation from the water column, favoring the accumulation of allochthonous C_{org} and fine sediment particles, and at reducing erosion and export. Due to their higher resistance to hydrodynamic forces, larger species also tend to form more stable and permanent meadows than small and ephemeral species (Duarte, 1991b; Mellors et al., 2002; Ondiviela et al., 2014).

As a consequence, large and persistent seagrass species generally show larger soil C_{org} deposits (Lavery et al., 2013; Rozaimi et al., 2016; Fig. 1a). Meadows formed by relatively small species may contain high C_{org} stocks if they occur in depositional areas (Lavery et al., 2013) although, due to their low below-ground biomass, most of the C_{org} sequestered is of allochthonous origin and thus relatively labile and vulnerable to remineralization compared to the C_{org} stored in meadows formed by large and persistent species (Enriquez et al., 1993; Lavery et al., 2013; Serrano et al., 2016).

3.1.2. Meadow canopy complexity

Even when formed by a single species, seagrass meadows differ in the complexity of their canopy, with important implications for their C_{org} sequestration capacity. Canopy complexity is defined as shoot density, leaf area and species-specific characteristics such as biomass (Samper-Villarreal et al., 2016) and represents a pool of sequestered C_{org} that will potentially accumulate in the soil compartment. As canopy complexity increases, the efficiency of seagrasses at reducing hydrodynamic energy and sediment resuspension is expected to be enhanced, particularly so in the case of seagrass with blade-like morphologies such as *Zostera or Thalassia spp.* (Verduin and Backhaus, 2000), leading to high particle trapping from the water column and to the formation of muddy soils (Koch et al., 2006, 2006; Hendriks et al., 2008; Peralta et al., 2008; Peterson et al., 2004).

Canopy complexity may also be enhanced by epiphytic algal assemblages that may account for up to 50% of the above-ground biomass (Borowitzka et al., 2006). As with other canopy features, these epiphytes likely affect hydrodynamics and particle trapping and often include large amounts of calcified algae which could contribute to both organic and inorganic C_{org} loading and soil accretion rates (Lavery and Vanderklift, 2002; Perry and Beavington-Penney, 2005).

Thus, higher canopy complexity is expected to lead to the formation of higher soil C_{org} deposits in seagrass meadows, as has been reported in recent studies (Samper-Villarreal et al., 2016; Serrano et al., 2016; Fig. 1b), but that effect may be more predictable in species with a blade-like morphology.

3.1.3. Seagrass landscape: patchy vs. continuous meadows

Seagrasses may form extensive and continuous meadows or patchy meadows, with different shapes and sizes of seagrass patches separated by unvegetated patches (Robbins and Bell, 1994). Seagrass landscape parameters include patchiness, patch size, and distance to patch edge. These parameters determine many ecological characteristics in seagrass ecosystems, such as associated biodiversity (Turner et al., 1999; Boström et al., 2006; Jackson et al., 2006), detritus transfer (Ricart et al., 2015), sedimentation patterns and sediment grain size distribution (Turner et al., 1999; Zong and Nepf, 2011; Ricart et al., 2017).

Recent studies suggest that continuous seagrass meadows are more efficient at soil C_{org} sequestration and storage due to a greater capacity to retain autochthonous C_{org} (i.e. leaf detritus) and to accumulate a higher proportion of finer sediments (i.e. silt and clay) (Miyajima et al., 2017; Oreska et al., 2017; Ricart et al., 2017). The magnitude of the soil C_{org} deposits inside the seagrass patches tend to increase with the distance from the seagrass-sand edge (Ricart et al., 2015; Oreska et al., 2017), indicating that large continuous meadows are more efficient at C_{org} storage (Fig. 1c).

3.1.4. Biotic interactions and the role of trophic webs

Interactions between seagrass plants and other organisms can be determinant of the capacity of seagrass meadows to sequester C_{org}. For example, grazers and burrowers not only benefit from seagrass productivity or protection (Orth et al., 1984; Siebert and Branch, 2007) but are also critical for the maintenance of meadows' health and thus for supporting all the ecosystem services they provide (including C_{org} sequestration). Both groups of organisms prevent the development of high levels of sulfide in seagrass soils (which may cause seagrass mortality) by inhibiting the accumulation of excessive detritus in seagrass soils and by enhancing soil oxygenation (Barber and Carlson, 1993; Carlson et al., 1994; Bertics and Zierbis, 2010).

However, dramatic increases in the population of grazers or burrowers may threaten C_{org} sequestration and storage in seagrass meadows. Overgrazing and increased burrower density has been described in situations where top-down control is absent, as occurs with the introduction of invasive grazer and burrower species or the demise of predator populations due, for example, to overfishing (Eklöf et al., 2008; Atwood et al., 2015; Lokko et al., 2015). Over-grazing may lead to a significant removal of the C_{org} stored as biomass (both above and below-ground) and thus to a lower accumulation of autochthonous C_{org} (Atwood et al., 2015). With overgrazing, leaves are shortened or removed and the capacity of the canopy to reduce water flow is expected to decrease, leading to a lower accumulation of allochthonous C_{org} from the water column and potentially higher exposure to erosional forces (Dahl et al., 2016). In addition, it may change meadow species composition favoring the dominance of small colonizer species (e.g. *Halophila* spp.) over larger species (Preen, 1995) which, as discussed above, generally reduces the C_{org} sequestration capacity of the meadows. On the other hand, increased bioturbation could also reduce C_{org} sequestration efficiency, as soil oxygenation will be favored and the remineralization of organic matter enhanced (Banta et al., 1999; Kirstensen, 2000), as suggested for saltmarsh soil C_{org} deposits (Coverdale et al., 2014; Martinetto et al., 2016) and seagrass meadows (Thomson, 2017).

Thus, shifts in predator-prey relationships due to top predator populations' extinction or the settlement of invasive grazer or burrower species in seagrass meadows may alter their capacity to sequester and store C_{org} in the long-term. All other factors being equal, meadows where complex and intact trophic webs are maintained are likely to show higher C_{org} storage capacity than ecosystems were trophic downgrading has occurred (Fig. 1d).
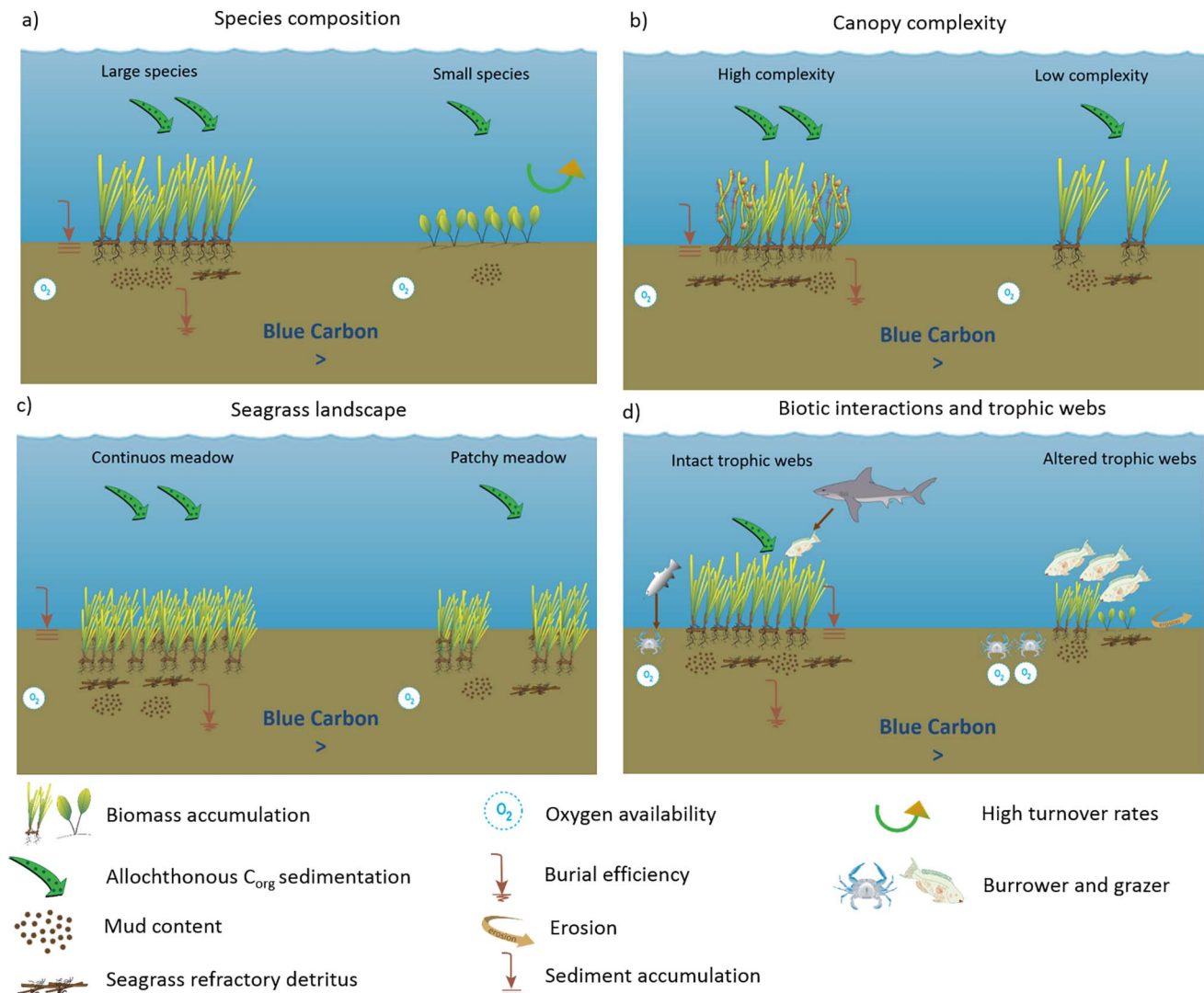
Fig. 1. Effect of biotic habitat characteristics on the formation of Blue Carbon deposits in seagrass soils through biomass accumulation, the input of allochthonous C_{org} and C_{org} burial efficiency (i.e. mud content, refractory organic matter and anoxic conditions). The effects of variation in (a) species composition and size, (b) canopy complexity, (c) seagrass landscape and (d) biotic interactions and trophic webs on soil C_{org} stocks and processes are shown. Diagram symbols are from the Integration and Application Network, University of Maryland Center for Environmental Science (http://ian.umces.edu/imagelibrary/).

3.2. Abiotic factors

3.2.1. Exposure to hydrodynamic energy

The degree of exposure to hydrodynamic forces such as waves, tides and currents, determines the patterns of sedimentation and erosion in coastal areas. In seagrass meadows, the level of exposure is usually reflected by the proportion of fine sediment particles, which is higher in sheltered areas compared to more exposed sites (van Keulen and Borowitzka, 2003). Thus, hydrodynamic energy is expected to affect C_{org} accumulation and storage in seagrass meadows through: 1) the balance between C_{org} (both autochthonous and allochthonous) accumulation vs. export; 2) the sediment grain size and the formation of muddy soils; and 3) the erosional patterns and the potential exposure to aerobic conditions of the already buried C_{org} (Burdige, 2007; Serrano et al., 2016). In meadows located in sheltered bays or estuaries and under calm conditions, sedimentation is typically enhanced compared to meadows located in more exposed sites, resulting in a higher content of fine sediment particles and larger C_{org} sedimentary deposits (Murphey and Fonseca, 1995; Fonseca and Bell, 1998; Röhr et al., 2016; Samper-Villarreal et al., 2016) (Fig. 2a).

Due to the close relationship between sediment grain size and hydrodynamics in coastal areas, sediment grain size is often used as a proxy of the hydrodynamic conditions in seagrass meadows (Cabaço et al., 2010; Mazarrasa et al., 2017a). Recently, the content of mud has been proposed as a useful indicator of the soil C_{org} stocks in seagrass meadows formed by small, fast growing species (e.g. Zostera spp. and Halophila spp.) (Dahl et al., 2016; Röhr et al., 2016; Serrano et al., 2016). In this type of meadows the contribution of autochthonous C_{org} to the soil deposits is low and the major C_{org} source is allochthonous organic matter that settles from the water column along with other fine mineral particles (Serrano et al., 2016). On the contrary, in meadows formed by large, long-living species, (e.g. Posidonia spp. and Amphibolis spp.), where the soil C_{org} deposits develop mainly through the accumulation of the large and recalcitrant below-ground biomass typical of these genera (Duarte and Chiscano, 1999; Klap et al., 2000), the soil's mud content is not a useful proxy of its C_{org} stocks or sequestration rates (Serrano et al., 2016).

3.2.2. Turbidity

Increased turbidity in coastal waters reduces irradiance, which is a primary factor controlling photosynthetic activity in seagrass meadows while determining seagrass distribution, growth and morphology (Duarte, 1991a; Lee et al., 2007). Several shading experiments demonstrate that the reduction of light availability leads to a decrease in
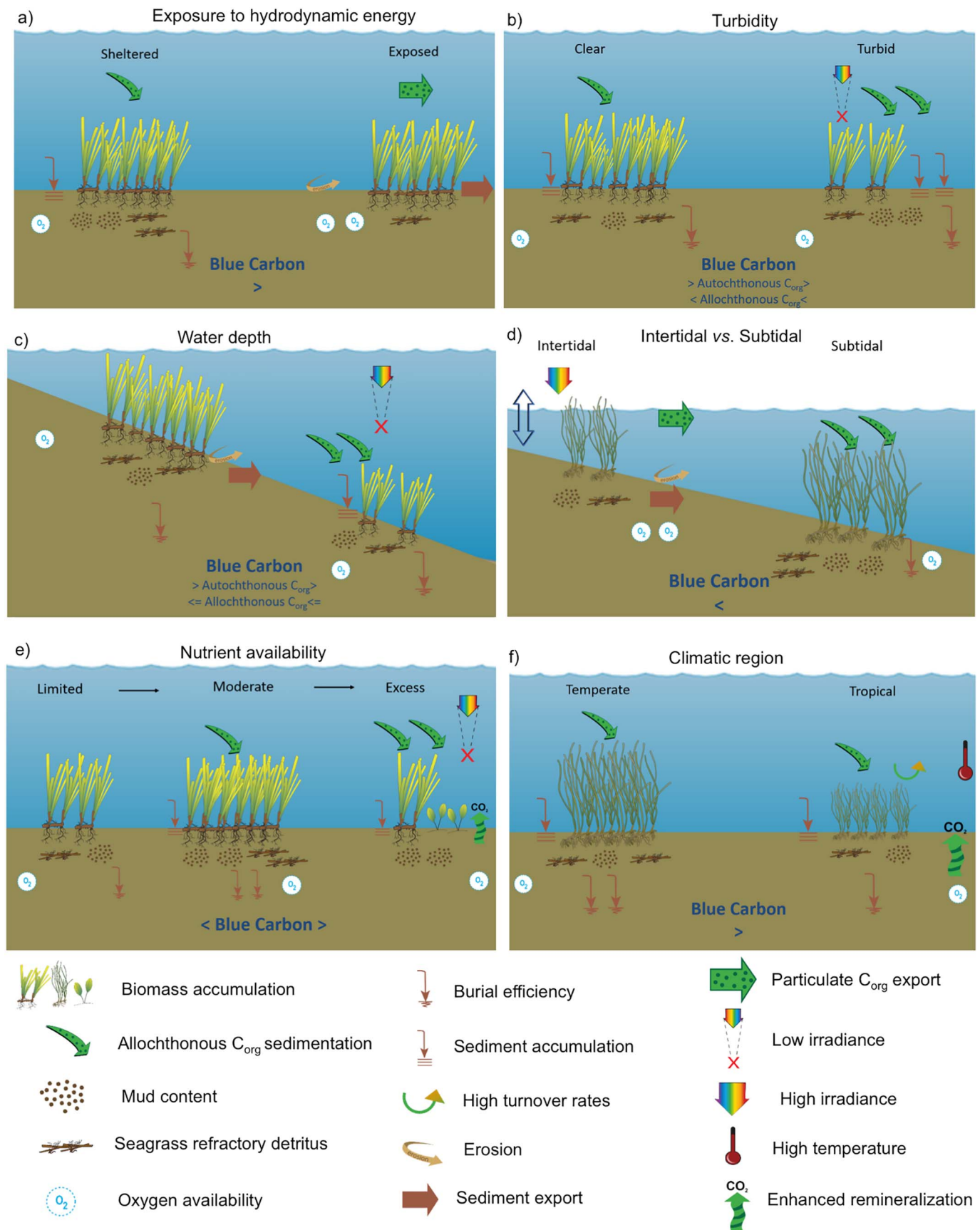
Fig. 2. Effect of abiotic habitat characteristics on the formation of Blue Carbon deposits in seagrass soils through seagrass biomass accumulation, the input of allochthonous C_{org} and C_{org} burial efficiency (i.e. mud content, refractory organic matter and anoxic conditions). The effects of variation of (a) exposure to hydrodynamic energy, (b) turbidity, (c) water depth, (d) intertidal vs. subtidal condition, (e) nutrient availability and (f) climatic region of soil C_{org} stocks and processes are shown. Diagram symbols are from the Integration and Application Network, University of Maryland Center for Environmental Science (http://ian.umces.edu/imagelibrary/).

shoot density and growth (Collier et al., 2009; Lavery et al., 2009; Ruiz and Romero, 2001) and field observations have confirmed this trend (Ruiz and Romero, 2003). As meadow biomass and shoot density decreases, the sequestration of autochthonous C_{org} decreases and, simultaneously, the capacity of the canopy to capture and retain allochthonous C_{org} from the water column is also reduced (Bos et al., 2007; Peralta et al., 2008). However, increased turbidity can potentially result in a greater accumulation of allochthonous C_{org} and fine sediment particles from the water column, leading to higher soil C_{org} accumulation rates and preservation after burial associated to low levels of oxygen concentrations in fine sediments (Samper-Villarreal et al., 2016; Serrano et al., 2016).

So far, there are only three studies that assess the effect of turbidity and light attenuation on seagrass soil C_{org} deposits (Table S1). Dahl et al. (2016) found that, after a five-month shading experiment, decreased irradiance led to lower C_{org} stocks in below-ground biomass but did not cause a significant effect in soil C_{org} stocks, likely due to the short duration of their experiment. Samper-Villarreal et al. (2016) found a significant increase in soil C_{org} stocks along a natural gradient of increasing turbidity that was partially explained by the enhanced stocks of allochthonous C_{org}. Yet, total C_{org} sequestration rates decreased as turbidity increased (Samper-Villarreal, 2016).

Thus, over a turbidity gradient, the largest sedimentary C_{org} stocks and sequestration rates (particularly of autochthonous origin) will likely occur in low turbidity environments as submarine irradiance, and presumably seagrass productivity, would be higher (Fig. 2b). However, enhanced accumulation of allochthonous C_{org} with increased turbidity may counterbalance the reduction in the input of autochthonous C_{org} and may result in similar, or even higher, C_{org} stocks in sedimentary deposits (Samper-Villarreal et al., 2016).

3.2.3. Water depth

Seagrass meadows are distributed from the intertidal zone to up to 40 m depth, mainly constrained by the availability of irradiance (Duarte, 1991a, 1991b). Similar to the effects caused by turbidity, light attenuation with water depth leads to a decrease in seagrass productivity, shoot density and growth (Alcoverro et al., 2001; Collier et al., 2007). Thus, it is reasonable to expect that C_{org} stocks and sequestration rates in seagrass soils would be higher in shallower meadows compared to deeper ones, as demonstrated in recent studies (Mateo and Romero, 1997; Serrano et al., 2014; Dahl et al., 2016; Serrano et al., 2016).

However, highlighting the complex interaction of factors that can drive C_{org} accumulation, increasing depth not only implies a reduction in irradiance but it also leads to changes in hydrodynamic conditions. Shallow meadows are, in general, more susceptible to wave action (Gambi et al., 1989; Koch et al., 2006, 2006) and, as a consequence, processes such as the export of seagrass detritus through soil erosion and subsequent soil aeration are favored whereas sedimentation might be reduced (Mateo and Romero, 1997; van Katwijk and Hermus, 2000; Koch et al., 2006, 2006). All these processes may contribute to enhance C_{org} deposits in deep seagrass meadows compared to shallower ones, as found by Lavery et al. (2013) in two meadows of *Posidonia sinuosa* and *Amphibolis antarctica*.

Thus, due to the attenuation of irradiance with depth and the associated reduction in seagrass productivity, density and cover (Weidemann and Bannister, 1986; Gallegos et al., 1990; Alcoverro et al., 2001), shallow subtidal meadows are, generally, expected to have larger soil C_{org} stocks and accumulation rates than deeper meadows, especially in terms of autochthonous C_{org} (Serrano et al., 2014, 2016) (Fig. 2c). Yet, significant differences in hydrodynamic conditions between shallow and deeper areas might disrupt this trend.

3.2.4. Intertidal vs. subtidal meadows

Intertidal meadows are subject to more extreme and variable environmental conditions than subtidal meadows, including intermittent exposure to air, higher irradiance, changes in water levels and generally higher hydrodynamic forces (i.e. wave action and tide currents) that lead to plants in these areas having different physiological and ecological traits (Grady, 1981; Pérez-Lloréns and Niell, 1993; Silva et al., 2005). The response of seagrass primary productivity to aerial exposure during low tide is complex and variable. Whereas some studies found that, during low tides, intertidal seagrass meadows can rapidly assimilate atmospheric CO_2 leading to comparable or even higher photosynthetic rates than in submerged conditions (Leuschner and Rees, 1993; Leuschner et al., 1998; Silva et al., 2005), others showed lower primary productivity and photosynthetic rates in aerial conditions compared to submerged conditions (Pérez-Lloréns and Niell, 1993; Clavier et al., 2011). CO_2 assimilation during periods of exposure to air seem to be constrained by the water content in seagrass tissue, with desiccation reducing carbon gains (Leuschner et al., 1998; Silva et al., 2005). Thus, the duration of emersion is a determinant factor of photosynthetic rates in intertidal seagrass meadows leading, generally, to higher growth rates and biomass in low intertidal meadows compared to high intertidal meadows (van Lent et al., 1991).

On the other hand, intertidal seagrass meadows are generally exposed to stronger hydrodynamic conditions that reduce their capacity to trap particles from the water column and their capacity to reduce erosion. Thus, lower mud and C_{org} contents are found in the soils of intertidal meadows compared to subtidal meadows (Grady, 1981; Heiss et al., 2000). In addition, intertidal meadows are expected to be affected by higher temperatures during emersion, that may enhance C_{org} remineralization, especially if strong hydrodynamic conditions lead to sediment suspension and oxygen exposure (Harrison, 1989; Burdige, 2007; Pedersen et al., 2011).

As a result, within the same species, intertidal meadows are expected to show lower soil C_{org} deposits and sequestration rates than subtidal meadows (Fig. 2d). However, the only available study that has assessed this effect did not find significant differences between the soil C_{org} stocks in intertidal and subtidal habitats (Lavery et al., 2013), providing evidence of the complex interactions in these environments.

3.2.5. Nutrient availability

Seagrass growth, abundance and morphology are strongly linked to nutrient availability (Short, 1987). Fertilization experiments show that seagrass meadows tend to be nutrient limited, with higher nutrient availability enhancing productivity, biomass, shoot length and density (Perez et al., 1991; Fourqurean and Zieman, 1992; Agawin et al., 1996; Lee and Dunton, 2000). Therefore, it is reasonable to expect that seagrass meadows in areas with a high nutrient availability would accumulate more autochthonous C_{org}. These meadows would also be more efficient at reducing water flow, thereby enhancing the accumulation of allochthonous C_{org} and fine sediment particles and reducing sediment erosion compared to meadows in oligotrophic waters. Yet recent studies revealed different effects of nutrient availability on the C_{org} stored in seagrass soils. Armitage and Fourqurean (2016) found an increase in the magnitude of the soil C_{org} stocks along a natural gradient of increasing phosphate availability in Florida Bay. In contrast, Howard et al. (2016) found no significant effect of increased nutrient availability, from natural fertilization, on the C_{org} stored in seagrass soils in a smaller area of Florida Bay, despite marked differences in the seagrass community structure and primary production. On the other hand, short-term experimental increases in nutrient availability have led to lower soil C_{org} stocks (Martínez-Crego et al., 2014; Armitage and Fourqurean, 2016) despite observed increases in the C_{org} content in below-ground biomass (Armitage and Fourqurean, 2016). This finding is likely related to an increase in microbial remineralization activity induced by the higher nutritional value of the seagrass tissues (Martínez-Crego et al., 2014) or to the short temporal and spatial scales of the experiments, that might have been insufficient to detect any positive effects of the increase in biomass C_{org} sequestration on the soil C_{org} deposits (Armitage and Fourqurean, 2016).

On the other hand, excessive nutrient availability often leads to changes in the species composition of seagrass meadows (Howard et al., 2016) enhancing the spread of fast-growing and "colonizer" species such as *Halophila* spp.*,* which, as described previously, are less efficient at sequestering autochthonous C_{org} than larger and persistent species. Nutrient enrichment can also lead to the proliferation of phytoplankton (i.e. eutrophication), epiphytes or macroalgae (McGlathery et al., 2007) that, when in excess, detrimentally affect seagrass productivity through competition for light and nutrients (Hauxwell et al., 2003), while increasing the amount of labile allochthonous C_{org} available to be trapped and stored in the soil C_{org} pool (Macreadie et al., 2012; Serrano et al., 2016). Furthermore, increased nutrient availability may enhance above-ground biomass relative to below-ground biomass (Lee and Dunton, 2000; Peralta et al., 2003), which is more vulnerable to export and grazing and is generally more labile than below-ground biomass (Klap et al., 2000; Macreadie et al., 2014).

Due to the potential complex interactions, the effect of nutrient availability on C_{org} accumulation in seagrass soils is still unclear. As suggested by Armitage and Fourqurean (2016), relatively high nutrient availability in oligotrophic coastal waters may lead to higher C_{org} storage in seagrass meadows if it affects sufficiently large areas over the long-term (e.g. decades). However, in excess or as a pulsed supply, nutrient inputs may compromise the long-term C_{org} sequestration capacity of seagrass meadows (Macreadie et al., 2017; Martínez-Crego et al., 2014) (Fig. 2e).

3.2.6. Climatic regions

Seagrasses are distributed across a broad range of latitudes encompassing a wide variability in temperature, irradiance and day length (Hemminga and Duarte, 2000; Olesen et al., 2015). Seagrass latitudinal variation has been related to differences in metabolic rates and ecosystem dynamics, with potential implications for C_{org} sequestration in seagrass soils.

Seagrass mean annual biomass and productivity tend to increase from lower to higher latitudes, particularly for above-ground biomass (Duarte, 1989; Duarte and Chiscano, 1999; Clausen et al., 2014), whereas biomass turnover rates tend to decrease from lower to higher latitudes (Duarte, 1989; Olesen et al., 2015). In general, temperate meadows show higher seasonal variability in biomass compared to tropical meadows (Duarte, 1989), suggesting a seasonal fluctuation in their C_{org} sequestration capacity, that would be higher during the productive, spring/summer season, particularly in the case of annual seagrass meadows (Bos et al., 2007). However, Clausen et al. (2014) found the opposite trend for *Zostera marina*, suggesting that latitudinal effects on seasonal C_{org} sequestration in seagrass biomass might vary among species. Thus, due to the higher biomass and productivity and the lower turnover rates showed by meadows at higher latitudes compared to meadows located at lower latitudes, we would expect higher soil C_{org} stocks in temperate meadows (Fig. 2f) although the seasonal variability in biomass observed at higher latitudes may disrupt this trend (Duarte, 1989; Duarte and Chiscano, 1999; Olesen et al., 2015).

On the other hand, high temperatures increase the rates of organic matter remineralization in seagrass soils (Pedersen et al., 2011) which could lead to lower C_{org} burial efficiency in tropical meadows compared to temperate ones. Yet, a recent study conducted in terrestrial soils suggests that across a latitudinal gradient, variation in the composition and total biomass of the microbial community is a more important determinant in the rate of remineralization of sedimentary organic matter than differences in temperature (Bradford et al., 2017).

To date, only two studies have addressed the effect of climatic regions in C_{org} storage in seagrass soils (Table S1). Lavery et al. (2013) did not find any significant variation of soil C_{org} stocks in 17 tropical vs. temperate Australian seagrass meadows, whereas Miyajima et al. (2015) found higher soil C_{org} stocks in temperate meadows compared to tropical and subtropical meadows from East and Southeast Asia. As both of those studies encompassed a broad range of seagrass meadows,

including different species and habitats, it is likely that the effect of temperature may have been confounded by other habitat factors acting at a smaller scale.

3.2.7. Future drivers of seagrass habitat: climate change and human pressure

Seagrass habitats are expected to vary in the near future due to climate change and increasing human pressures in coastal areas (Duarte, 2002). Among climate change consequences, we consider sea level rise, ocean acidification and increasing temperature (including extreme heat events) as the most relevant for C_{org} sequestration in seagrass meadows.

Sea level rise will lead to an increase in water depth and a subsequent reduction in submarine irradiance, not only due to increasing water depths but also due to potential increase in suspended sediments arising from coastal erosion, at least in the short-term. This will likely lead to the reduction of seagrass net primary production and seagrass C_{org} sequestration in deeper waters, possibly compensated by potential expansion of the meadow upslope on the landward edge (Saunders et al., 2013). Sea level rise might, in contrast, enhance C_{org} sequestration by intertidal seagrass meadows in some regions where the increase in low tide is expected to be higher than in high tide as the emersion and desiccation periods will be shortened (Short and Neckles, 1999).

The global increase in sea temperature is likely to lead to changes in seagrass species distribution and metabolic and dynamic features (e.g. phenology, annual mean biomass, productivity, or turnover rates) (Clausen et al., 2014; Hyndes et al., 2016). Specifically, warming of temperate regions could lead to a reduction of seagrass biomass and productivity and an increase in turnover rates (Duarte, 1989; Duarte and Chiscano, 1999; Clausen et al., 2014; Olesen et al., 2015), with the subsequent reduction in net autochthonous C_{org} sequestration. However, ocean warming could enhance seagrass meadows expansions towards northern latitudes, such as the Arctic region, as has been suggested for eelgrass species, leading to new seagrass-based Blue Carbon ecosystems (Krause-Jensen and Duarte, 2014). Yet, seagrass expansion to the Arctic region may be limited by propagule supply, as dispersal through seeds is constrained by failure to complete the reproductive cycle in northernmost populations under the present low temperatures (Krause-Jensen and Duarte, 2014).

On the other hand, episodic high temperature anomalies have been shown to result in extensive death of temperate/sub-tropical seagrass meadows (Díaz-Almela et al., 2009; Marbà and Duarte, 2010; Fraser et al., 2014). In addition, the success of sexual reproduction in seagrass meadows, that enhances their resilience against environmental changes, shows contradictory responses to heat waves: whereas flowering seems to be enhanced (Diaz-Almela et al., 2007; Ruiz et al., 2017), seed survival has been found to be negatively affected (Thomson et al., 2014). In addition, increasing temperature is expected to enhance the activity of seagrass soil microbial communities that would lead to higher C_{org} remineralization rates in seagrass soils (Pedersen et al., 2011) and to a lower C_{org} sequestration efficiency.

Ocean acidification could potentially increase the sequestration of autochthonous C_{org}, as suggested by recent studies that report an increase in above- and below-ground biomass under acidified conditions (Palacios and Zimmerman, 2007; Hall-Spencer et al., 2008; Fabricius et al., 2011; Russell et al., 2013). However, the only available study that assessed the effect of acidification on seagrass soil C_{org} deposits reported a significant negative effect (Martínez-Crego et al., 2014).

Finally, the increase in human pressure in coastal areas, particularly during the last century (Duarte, 2014), is leading to an increase of nutrient and terrestrial sediments loading into coastal waters, causing detrimental effects in seagrass meadows and associated C_{org} deposits (Orth et al., 2006; Ralph et al., 2006; Macreadie et al., 2012). Eutrophication and increased turbidity threaten seagrass meadows survival (Nixon, 1995; Short and Wyllie-Echeverria, 1996; Waycott et al., 2009) and favor the accumulation of allochthonous C_{org} (e.g.

microalgae-derived Corg) into the soil deposits, as reported in recent studies (Macreadie et al., 2012; Serrano et al., 2016; Mazarrasa et al., 2017b; Samper-Villarreal et al., 2018). Although the enhanced accumulation of allochthonous C_{org} may lead to an increase in the total C_{org} sequestration in seagrass meadows under high human pressure (Serrano et al., 2016; Mazarrasa et al., 2017b; Samper-Villarreal et al., 2018), it may also lead to the weakening of the soil deposits due to its higher lability and vulnerability to remineralization compared to seagrass-derived C_{org} (Enriquez et al., 1993; Macreadie et al., 2012). In addition, enhanced nutrient supply may trigger soil microbial activity leading to the acceleration of C_{org} remineralization rates (Macreadie et al., 2017). Finally, the increase in human pressure in coastal areas is also leading to seagrass habitat fragmentation (Montefalcone et al., 2010), that negatively affects C_{org} sequestration and storage in seagrass soils (Oreska et al., 2017; Ricart et al., 2017).

Thus, it is apparent that climate change and increased human pressure in coastal areas generally threaten the role of seagrasses as long-term carbon sinks. The effect of ocean acidification is still to be clarified.

4. Key habitat characteristics enhancing C_{org} sequestration in seagrass meadows and future research

The analysis conducted in the previous sections demonstrates that not all seagrass meadows have the same potential for long-term C_{org} sequestration and storage and that habitat characteristics strongly influence this function. It is also apparent that the accumulation of autochthonous C_{org} (i.e. derived from seagrass biomass) and the input of allochthonous C_{org} usually show different responses to habitat settings, particularly to abiotic factors. For instance, turbidity leads to lower biomass productivity and accumulation but enhances allochthonous C_{org} accumulation. The largest C_{org} deposits (particularly of autochthonous C_{org}) usually occur in continuous meadows formed by large and persistent species with complex canopies and when located in sheltered, shallow, low energy and clear environments with low/mid nutrient inputs (Figs. 1 and 2). However, large C_{org} deposits formed, mainly, by allochthonous C_{org}, can also be found in meadows formed by small and colonizer species, located in sheltered and depositional bays where the soil mud content will be a good proxy of the soil C_{org} deposits (Serrano et al., 2016). Habitats where trophic webs have been disturbed and where there is a lack of top-down control may show lower C_{org} deposits and sequestration rates due to overgrazing or an excessive bioturbation (Atwood et al., 2015; Macreadie et al., 2017) (Fig. 1d). Finally, meadows under high and increasing human pressure are likely to experiment a decline in their capacity to sequester and store C_{org} in the long-term due to habitat fragmentation, eutrophication and the weakening of the soil C_{org} deposits (Montefalcone et al., 2010; Macreadie et al., 2012; Macreadie et al., 2017; Ricart et al., 2017).

The general conclusions presented above are based on a scarce number of studies available, particularly limited in the case of restored meadows (Table S1). In addition, few studies report C_{org} sequestration rates along with, or instead of, C_{org} stocks, which limits our ability to resolve relationships between habitat characteristics and C_{org} sequestration in seagrass meadows. C_{org} stocks provide information on the magnitude of the sedimentary deposits and potentially avoided GHG emissions following meadow disturbances but they do not necessarily indicate the current state of a carbon sink (i.e. if it is being sequestered or released; Macreadie et al., 2014). Thus, further research is needed in order to better understand the effect that the variability in habitat settings have in the capacity of seagrass meadows to act as carbon sinks. Research efforts should be especially addressed to measure C_{org} sequestration rates under different habitat settings, considering both preserved and restored meadows, and to resolve the effect of those factors with unclear effects. We identified the variability on carbon sinks due to intertidal vs. subtidal positions, the implications of climatic region, the potential impact of ocean acidification, and the effects of

Table 1
Summary of habitat characteristics that have a favorable effect on the long term C_{org} storage in seagrass soils, those that threaten this function and those whose effect is still unresolved, based on the review of Blue Carbon research conducted in this study.

Effect	Habitat parameter	Indicator
Favorable	Species composition	Dominated by large species
	Canopy complexity	High
	Meadow landscape	Continuous
	Biotic interactions	Complex and stable trophic webs
	Exposure to wave energy	Sheltered
	Turbidity	Low
	Water depth	Shallow except if exposed to high hydrodynamic energy
	Nutrient availability	Low but not limited
Threat	Altered trophic webs: lack of predators	Over grazing, excess bioturbation
	Human pressure	Eutrophication, habitat fragmentation
	Climate change	Temperature increase and sea level rise
Unresolved	Intertidal vs. subtidal	
	Climatic region	
	Acidification	

nutrient enrichment as key gaps in our understanding of the habitat factors determining C_{org} sequestration (Table 1). Importantly, the interactive effects of multiple factors acting on C_{org} sequestration needs to be evaluated, a complex issue that may benefit from modeling approaches.

5. Implications for the implementation of Blue Carbon strategies

Conservation and restoration of seagrass meadows contributes to climate change mitigation through the sequestration and preservation of Blue Carbon. Conversely, Blue Carbon may be used by managers as a tool to enhance seagrass conservation and restoration. This could be achieved by obtaining financial support (e.g. carbon credits, Emmer et al., 2015), by promoting the consideration of seagrass meadows within national GHG accounting schemes and reduction targets (Herr et al., 2017) or as an additional value to be considered, along with other ecosystem services and biodiversity targets, when planning the creation of marine protected areas or when selecting cost-effective areas for seagrass restoration projects (Adame et al., 2015; Howard et al., 2017).

Through the analysis conducted in the previous sections, we identify certain aspects that should be taken into account when developing and implementing efficient climate change mitigation strategies based on seagrass meadows: the large heterogeneity of C_{org} deposits and sequestration rates across habitats and the need to use site-specific C_{org} storage values; the different responses of autochthonous and allochthonous C_{org} to habitat factors; and how climate change and human pressure potentially affect C_{org} sequestration in seagrass soils.

The use of site specific values of C_{org} storage instead of values from the literature should be encouraged whenever possible (IPCC, 2013; Emmer et al., 2015). Using values derived for specific sites or derived from comparable habitats elsewhere will reduce the likelihood of over- or under-estimations of C_{org} stocks and sequestration rates, as has been recently suggested (Oreska et al., 2017).

The different responses of the autochthonous and allochthonous C_{org} pools to habitat characteristics identified in this study needs to be considered, as it has important implications for the efficiency of climate change mitigation strategies. Due to its higher lability, high levels of allochthonous C_{org} accumulation may compromises the stability of the sedimentary C_{org} deposits in the long-term. Thus, habitat settings that favor the accumulation of autochthonous C_{org} rather than allochthonous C_{org} are expected to lead to stable C_{org} deposits. In contrast, meadows where the accumulation of allochthonous C_{org} is high will lead to the formation of more vulnerable carbon sinks that, in the case of meadow degradation, have a higher potential to be remineralized

and released as CO_2 to the atmosphere. In addition, allochthonous enriched C_{org} soil stocks are often found in meadows under a high level of anthropogenic and urban pressure (Mazarrasa et al., 2017b). These meadows are threatened by different impacts caused by human activities (e.g. dredging, eutrophication), increasing the risk of meadow degradation and CO_2 emissions from the remineralization of the sedimentary C_{org} deposits. The allochthonous C_{org} pool is currently not considered under the available C_{org} accounting scheme for seagrass restoration projects (Verified Carbon Standard, Emmer et al., 2015) due to the risk of double accounting. Yet, due to its significant contribution to some seagrass soils and its vulnerability to remineralization, we consider it critical that the allochthonous C_{org} pool is incorporated in future carbon accounting schemes to avoid the risk of neglecting the protection of large C_{org} soil deposits particularly vulnerable to remineralization.

Finally, the effect that human pressure and climate change may have in the C_{org} sequestration of seagrass meadows should also be taken into account when designing the implementation of Blue Carbon strategies. Managing direct, local human impacts may provide significant opportunities for buffering the effects of those factors that threaten C_{org} sequestration in seagrass meadows and for increasing and preserving their C_{org} sequestration capacity in the future. For instance, reducing nutrient loading to coastal waters (Saunders et al., 2013; Macreadie et al., 2017) or regulating activities that lead to habitat fragmentation (e.g. dredging, boat anchoring) or to the extinction of top-predators (i.e. overfishing; Atwood et al., 2015) will help to maintain C_{org} sequestration and long-term storage by seagrass meadows. Sea-level rise could be buffered by limiting the impacts of coastal urbanization and by restoring natural wetlands, allowing seagrass to expand upslope along the landward edge (Macreadie et al., 2017). However, the effect of other climate change consequences, such as ocean acidification and increasing temperature on the C_{org} sequestration capacity of seagrass meadows are less clear and more difficult to manage locally but should, at least, be recognized when planning the implementation of Blue Carbon strategies (UNEP, CIFOR, 2014).

In this review we have focused on the relative capacity of different seagrass habitats to sequester C_{org} in the long-term. Managers or proponents of Blue Carbon projects should take these differences among habitats into account but they should not be the sole criteria considered as carbon sequestration and storage is only one of the many ecosystems services which managers should seek to conserve. Habitats with lower C_{org} sequestration and storage capacity may be valued for a range of other ecosystem services and although Blue Carbon may be lower compared to other seagrass habitats, it may strengthen the argument for their conservation and provide a means of partially funding conservation measures (Adame et al., 2015; Howard et al., 2017).

6. Conclusions

Through the review of the most recent literature on seagrass Blue Carbon research we have identified the habitat settings that are likely to enhance or reduce the C_{org} sequestration capacity in seagrass meadows, those that may threaten this function and the gaps of knowledge that need to be addressed. The findings of this review may provide guidance to managers aiming to support seagrass conservation and restoration, to policy makers willing to enhance the implementation of efficient Blue Carbon strategies and to the scientific community aiming to resolve uncertainties on the habitat characteristics that govern the carbon sequestration capacity of seagrass meadows.

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